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ON THE DISPERSAL BY FLIES OF THE SPORES OF CERTAIN MOSSES OF THE FAMILY SPLACHNACEAE[1]

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During my stay in the Adirondacks last summer (1920) I had an opportunity to observe on the summit of Mt. Skylight, above timberline, two species of Splachnaceae: *Tetraplodon mnioides* B. & S., and *T. angustatus* B. & S.[1] They were growing on the droppings of some carnivorous mammal, among the sphagnum of the boggy slopes. Both species are of course known to occur in the Adirondack region, though the smaller of the two, *T. angustatus*, is said to be much rarer than the other. The finding of these mosses, however, resulted in an interesting ecological observation, quite new to me at the time and well worth recording.

The object of my trip to Mt. Skylight was primarily of an entomological nature and, though I incidentally gathered some bryological material, the *Tetraplodons* would probably have been overlooked had my attention not been attracted by some small flies that flew up from one of the mosses as I was moving in the bog. On closer examination of the object which these insects had left, much to my surprise I found it to consist of a cushion of *Tetraplodon mnioides* with abundant, bright brown-red fructifications. That this moss could be attractive to flies struck me as most remarkable and I proceeded to watch the plants more carefully. Soon some of the insects returned to the little moss-cushion; alighting on the upper end of the capsules, they moved downward to reach the upper part of the hypophysis, going from one capsule to another. On approaching a hand lens as unobtrusively as possible, I could distinctly see the flies passing the soft labella of their proboscis over the upper part of the hypophysis, much like house-flies feeding on sugar, meat, or the perspiration of human skin. It was thus quite evident that the flies visiting the hypophyses of *Tetraplodon* lick up a secretion produced by that part of the plant. When disturbed they fly off, rest a little distance away, and shortly return to the moss capsules, so that the drawing power exercised on them by the hypophyses of this *Tetraplodon* is by no means accidental. In alighting or in leaving, the tiny creatures inevitably touch the spores at the mouth of the capsules, when these are ripe and opened. Thus some of the spores become attached to the hairs, the legs, or other parts of the flies and are eventually carried off by them.

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[1] I am greatly indebted to my friend, Dr. W. H. Wiegmann, of New York City, for the identification of these mosses.

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A more detailed examination of the capsules shows a large number of gigantic stomata of the phaneropore type crowded into the upper half of the hypophysis, in the very region so actively sought by the flies. According to Dr. Wiegmann these are the largest superficial stomata he has seen in any species of moss: they measure with their guard cells .051 × .042 mm., while their opening is .021 × .003 mm.; they can readily be detected with a × 10 hand lens. Transverse and longitudinal sections of the hypophysis show below the stomata a great abundance of cells rich in chlorophyll. It is probable that from these stomata exudates the secretion which is lapped up by the flies.

The flies captured while licking the hypophyses of *Tetraplodon mnioides* were both sexes of a small anthomyid belonging to the genus *Phorbia.*[2] I believe, however, that other muscid and anthomyid flies with short proboscis and soft labella are also attracted by the capsules of this and other *Splachnaceæ.*

The facts related above were quite new to me at the time. Meanwhile, however, I have found that N. Bryhn, in Norway, has given an account of similar relations between flies and certain European *Splachnaceæ.* Since my interpretation differs in some respects from Bryhn's, a brief abstract of his interesting paper[3] may not be out of place here. His first observations were made with *Splachnum rubrum,* an arctic species which grows on the excrement of cattle. On a sunny day he noticed that a cushion of this moss attracted a swarm of flies, some much like house-flies, also dung-flies and blow-flies,[4] which alighted on the cushion and crawled over the apophyses of the moss. In a half hour he counted over 50 visits of flies to one cushion. Some of these insects were caught and all were found to be covered with a yellow powder, which, upon microscopic examination, proved to consist of spores of *Splachnum.* The flies either were powdered uniformly over the under side, or they carried a large patch of spores on the thorax. Bryhn also noticed that the flies upon leaving the cushion of *Splachnum* often flew to fresh cow-dung nearby and wandered over it. He thus came to the conclusion that they sow the spores of this moss and further observations with other species of *Splachnum* and *Tetraplodon* confirmed this view. He also succeeded in making the spores of *Splachnum rubrum* germinate on fresh cow-dung.

The *Splachnaceæ* present in their mode of fructification many peculiarities which, according to Bryhn, greatly facilitate the dispersal of their spores through the agency of flies. In the case of *Splachnum,* for instance, a number of plants form dense and rather large cushions, which are as much as 25 cm. across and quite showy even from a distance. The seta is very long (as much as 20 cm.)

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[2] These flies were kindly identified by Mr. J. A. Aldrich, Associate Curator at the U. S. National Museum.

[3] Bryhn, N. Beobachtungen über das Ausstreuen der Sporen bei den Splachnaceen. Biologisches Centralblatt. **17**: 48–55. 1897.

[4] Bryhn's terms are "Dungfliegen" and "Schmeissfliegen." Since no scientific names are used it is difficult to know exactly what kind of flies are meant. Perhaps his "Dungfliegen" were species of *Scatophaga,* while the "Schmeissfliegen" were probably of the common *Calliphora vomitoria.*

and grows even after the spores are ripe. The neck of the capsule is swollen into a hypophysis much larger than the capsule itself; size, shape and color of this hypophysis are variable, but characteristic for each species. In all cases, however, the hypophysis becomes bright colored about the time the spores are ripe, but even thereafter it continues to grow for a time, so that the plant becomes larger and showier the longer it lives. The capsule and its peristome are very hygroscopic; its central columella is widened at the tip into a small disk. When the capsule is ripe, the operculum falls off and, in dry weather, the teeth of the peristome curve outward over the margin of the capsule, which shrivels and contracts, while the columella extends beyond the rim. The spores are thus pushed upward along the columella against its terminal disk, and drop partly outside the capsule on the expanded teeth of the peristome. Most other moss spores are dry and powdery, and easily transported by the wind, but in *Splachnum* they are sticky and form small clusters which remain attached between the columella and margins of the capsule and also on the expanded peristome. They are thus freely exposed and ready to adhere to any part of a fly that may pass over them. In a moist atmosphere the capsule swells again to its former shape and size, and takes the spores back into its cavity, while the teeth of the peristome fold back to close the mouth of the capsule as with a lid, so that rain or dew can not wash the spores away and rob the plant of their use.

In *Tetraplodon* the hypophysis is not so bright colored, but here too, it continues to grow after the spores are ripe; the seta of mature capsules, however, does not grow further. These mosses being perennial, their cushions become much larger and showier than those of *Splachnum*, The columella is crowned with the detached tips of the peristomial teeth, but does not extend beyond the margin of the shriveled capsule. Since the seta is shorter and often also thicker and stiffer than in *Splachnum*, it can support larger insects, such as blow-flies.

From my own observations and those of Bryhn we may conclude that many, if not all, *Splachnaceæ* are adapted to having their spores scattered by flies. In the first place the various members of the family are found growing only on decaying organic substances, such as excrement and dead bodies. As shown experimentally by Bryhn, their spores do not germinate on other substrata. Excrement and dead bodies, however, are comparatively scarce in nature, always considerably scattered over a wide territory, and often hidden in crevices. If, as in other mosses, the spores of the *Splachnaceæ* were carried by the wind, they would have but little chance of reaching the proper substratum. That they are not transported in this way is further shown by their stickiness. They adhere readily, however, to the muscid and anthomyid flies which are constant visitors both to the fructifications of these mosses and to dung and carrion.

Bryhn is still uncertain as to the manner in which the flies are attracted to the moss. He supposes that the beautiful cushions may serve as a "playground" for them, or as resting places between flights. "Most probably," he continues, "the flies are deceived by the bright colors and suppose that the moss is a collection of melliferous flowers or perhaps, better still, one of the large mushrooms, some species of which possess somewhat similar, though not quite as bright colors. The shape of a *Splachnum* cushion viewed as a whole from a distance reminds one somewhat of one of the large mushrooms which are much liked by flies. On two occasions I found an ant inside the hypophysis of *Splachnum vasculosum*. These ants were undoubtedly intent upon stealing honey; they had bitten an opening, crawled inside and were fooled. And what can deceive an ant, could easily do the same with a fly."[5] Commenting upon Bryhn's observations, Goebel[6] supposes that the luster, rather than the color of the hypophysis is the main attraction, since it is known that shiny objects are very alluring to flies. Goebel further calls attention to the peculiar odor emitted by *Splachnum*, which may also invite the insects.

I have also noticed the very strong and characteristic odor of fruit-bearing cushions of *Tetraplodon mnioides*. It is my opinion that this redolence, as in the case of flowers, is the main attractive agent, at least at a certain distance. It is a well established fact that the olfactive powers of insects are very highly developed. On approaching nearer to the cushions, the flies may then be able to locate the source of the fragrance by the bright and shiny hypophyses. I do not think, however, that they are in the least "fooled" by the moss cushions, for I have observed them licking the surface of the hypophysis. Furthermore, if deceived, they would not return so readily to the same spot when disturbed. The dispersal of the spores of *Splachnaceæ* by flies is, in my estimation, the complete parallel of the cross-pollination of many flowers by insects. In both cases the plant not only possesses certain devices to allure its agents, but also offers food either for them or their young, thus causing them to be steady visitors.

The *Splachnaceæ* are thus far the only bryophytes for which a dispersal of spores by insects has been indicated.[7] Additional observations on the indigenous and exotic members of the family would therefore be welcome to the ecologist and it is hoped that students of mosses will further investigate this interesting topic.

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[5] That the ants in this case were "fooled," as Bryhn expresses it, is by no means certain. I rather believe that they were attracted by the soft and swollen hypophysis and were enjoying a feast on its juices. These insects could, however, not be of much use in the dispersal of the spores, for it is not likely that they would transfer them to fresh dung or carrion.

[6] Goebel, K. Organographie der Pflanzen. 2d Ed. Bd. II, Heft 1, 889–890. 1915.

[7] C. C. Plitt (BRYOLOGIST **10:** 54–55, 1907) has noted that ants are fond of the spores of *Webera sessilis;* he also found the capsules of this moss gnawed on a patch growing over an ant's nest. That these insects would be effective scatterers of the spores of this moss seems extremely doubtful.